

# SPATIAL AND TEMPORAL PATTERNS IN FERTILIZATION AND SETTLEMENT OF YOUNG GAG (*MYCTEROPERCA MICROLEPIS*) ALONG THE WEST FLORIDA SHELF

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## ABSTRACT

We used otolith analyses of juvenile gag, *Mycteroperca microlepis* (Goode and Bean, 1879) settling in seagrass beds along the west Florida coast over a 4-yr period (1994 through 1997) to examine regional and temporal differences in fertilization date, pelagic larval duration, and settlement date. We found annually consistent geographic patterns in the mean fertilization and settlement dates of juvenile gag. These dates were several weeks earlier for fish recruiting south of 28° N than they were for fish recruiting north of 28° N. While it was beyond the scope of this study to determine the processes responsible for these patterns, we consider several possible mechanisms that might account for the patterns we observed. These include (1) a north-south difference in spawning times, (2) a year-to-year change in wind-driven surface currents affecting distribution during the pelagic larval phase, and (3) a north-south difference in seagrass habitat available to settlers. The patterns did not appear to result from differences in spawning time, seasonal changes in wind driven surface currents, or seagrass habitat availability. However, both pelagic larval duration and the time differences between west Florida gag populations and those from Campeche Bank are consistent with the appearance of earlier-spawned juveniles in south Florida. Transport from Campeche Bank is possible via the Loop Current. Our modeling of onshore movement considered only the wind forcing of the surface layer, essentially a two-dimensional model. A three-dimensional model would be useful to evaluate transport at various depths.

Understanding recruitment processes of warm-temperate reef fishes such as grouper (Family Serranidae) is crucial in light of the vulnerability of reef fish populations to intense fishing pressure. Such pressures may result in demographic changes involving size, age, and sex ratio; recruitment overfishing; and dramatic population declines (Coleman et al., 1996, 2000; Rogers and Beets, 2001; Sala et al., 2001). When fishing negatively affects reproductive attributes of a population, the fishery biomass available for capture increasingly depends on the strength of recruitment and survival through early life history (Smith, 1993). Gag, *Mycteroperca microlepis* (Goode and Bean, 1879), lends itself well to studies of recruitment because: (1) the West Florida Shelf appears to be the primary spawning source for gag populations in the north-eastern Gulf of Mexico (Schirripa and Legault, 1997; Koenig et al., 2000; Turner et al., 2001), (2) the population may be self-recruiting (Heinisch and Fable, 1999), and (3) juvenile population abundance inshore can be quantified (Koenig and Coleman, 1998).

The principal spawning habitat for gag in this region is high relief hardbottom along the continental shelf edge (70–90 m deep; Moe, 1963; Coleman et al., 1996; Koenig et al., 2000), where peak spawning occurs in February and March (Hood and Schlieder, 1992; Collins et al., 1998). The dominant nursery habitat for gag includes

high salinity seagrass meadows of shallow coastal waters (Koenig and Coleman, 1998) ranging from 70 to 600 km away.

Mortality rates of juveniles are low during their estuarine phase (Koenig and Coleman, 1998). However, regional juvenile abundance can vary over 200 fold between high ( $1085 \text{ ha}^{-1}$  in 1993) and low ( $3.9 \text{ ha}^{-1}$  in 1990) settlement years (Koenig and Coleman, 1999; unpubl. data). Such variation correlates strongly with year-class strength in the fishery. Strong year classes detected in the landings are relatively episodic, but when they occur, they can overwhelm other year classes in the catch (Fitzhugh et al., 2003).

In this study, we determined for gag the temporal variation in spawning, fertilization, larval settlement, and pelagic larval duration (PLD, the period between fertilization and settlement), as well as the seasonal variability in juvenile habitat conditions along the west Florida coast. We examined these spatially in two regions, one north and the other south of  $28^\circ \text{ N}$  latitude, the demarcation line separating two distinct zoogeographic regions of west Florida coastal waters (Smith, 1976; Hoese and Moore, 1998). The intent was to evaluate these data for seasonally and/or temporally consistent patterns that might reveal the underlying mechanisms driving differences in recruitment. We considered three possible mechanisms that could explain the recruitment patterns we observed (based on the assumption that gag recruits to the west Florida coast result from spawning events occurring on the West Florida Shelf): (1) spawning time differences for adult gag along the West Florida Shelf, (2) regional differences in suitable settlement habitat (in this case, seagrass beds), and (3) seasonal changes in wind-driven surface currents that might support larval transport. We investigated horizontal transport by oceanic currents using an empirical model, calibrated by surface-drifting buoys, of near-surface transport forced by daily winds. We did not evaluate vertical movement patterns because these are essentially unknown for gag larvae, which are rare in ichthyoplankton surveys of the northeastern Gulf of Mexico (conducted by the National Marine Fisheries Service).

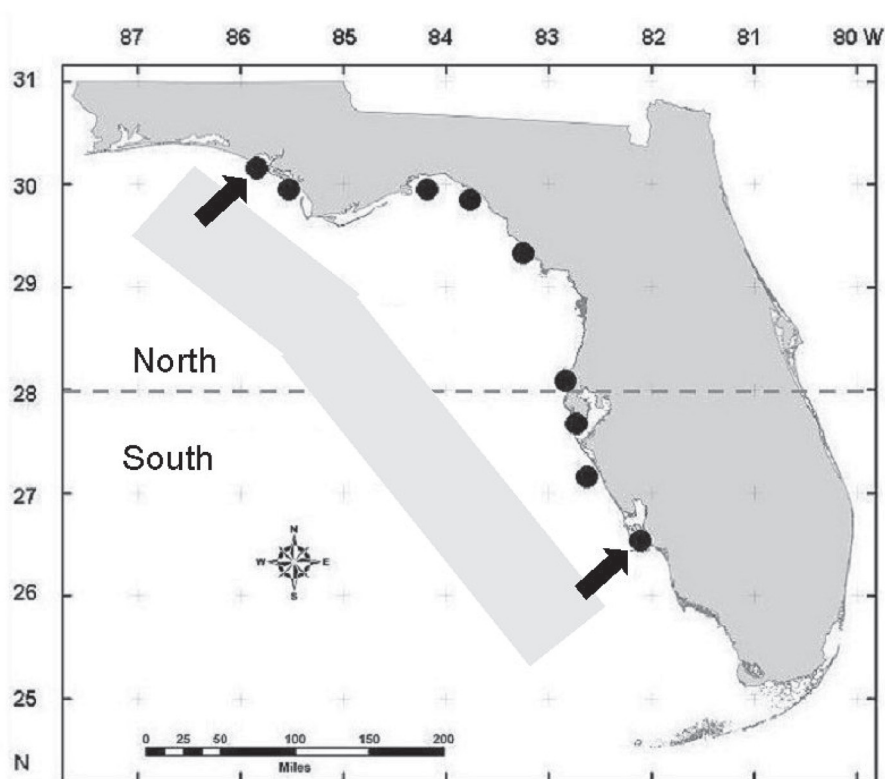
## METHODS

### FERTILIZATION AND SETTLEMENT CHARACTERIZATION

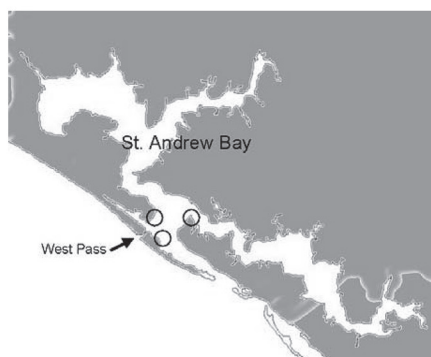
*Field Sampling.*—We collected juvenile gag from nine locations (encompassing 20 stations) distributed north and south of  $28^\circ \text{ N}$  in large, dense seagrass beds of West Florida coastal waters (Fig. 1). The northern region includes the Big Bend and the Florida Panhandle and extends to the northwest extreme of significant seagrass habitat in the eastern Gulf of Mexico (St. Andrew Bay,  $\sim 30^\circ \text{ N}$ ). The southern region includes Peninsular Florida, extending south from  $28^\circ \text{ N}$  to the most southern extent of significant seagrass habitat (Pine Island Sound,  $\sim 26^\circ \text{ N}$ ). No sampling occurred west of St. Andrew Bay because seagrass in that area is sparse and does not support significant numbers of recruiting juveniles (Koenig, pers. obs.). Nor did sampling occur south of Pine Island Sound because most of the seagrass of that area, particularly around Florida Bay, has undergone significant anthropogenic change since the late 1980s that severely reduced its significance as nursery habitat for juvenile reef fish (Butler et al., 1995).

From 1994 through 1997, juvenile fish were collected systematically (every other month) throughout the west Florida coast, beginning in late February or early March and continuing through early October, when juveniles egress offshore (Koenig and Coleman, 1998). We sampled juveniles using two gear types: a benthic scrape ( $1.0 \text{ m wide} \times 0.4 \text{ m high}$  stainless steel frame, 2 mm mesh tailbag) and an otter trawl (5 m trawl, 3 mm mesh tailbag). The benthic scrape allowed capture of the smallest (15–25 mm standard length, SL) post-settle-

A



B



C



Figure 1. A) Adult spawning areas (light grey boxes) and juvenile sampling locations (black circles) for gag *Mycteroperca microlepis* in the Gulf of Mexico from 1995 to 1997. Dotted line indicates regional separation of sampling sites north and south of 28° N. B) Replicate sampling stations within St. Andrew Bay. C) Replicate sampling stations within Pine Island Sound.

ment juveniles unavailable to the otter trawl. The otter trawl captured larger individuals (> 50 mm SL). Otter trawl tows were approximately 150 m (duration = 5 min, tow speed = 1.0 kt) and benthic scrape tows were approximately 50 m, also at 1.0 kt ( $N = 5$  replicates per station, avoiding previously towed areas). Samples were collected diurnally and primarily during flood tides. Shorter tows occurred when drift algae clogged nets. These were not included as standard tows.

Juvenile gag collected from each tow were bagged and stored on ice, and then frozen for storage at the end of a sampling trip. Before otolith extraction, fish were thawed, measured to the nearest mm SL, weighed to the nearest 0.1 g, and lapillus otoliths extracted.

*Juvenile Densities.*—Multiple standard otter trawl tows were made at the nine sampling locations several times during the summer of each year. We based density estimates of juvenile gag on standard otter trawl tows that each sampled about 300 m<sup>2</sup> of seagrass with a capture efficiency of about 40% (Koenig and Coleman, 1998). Juvenile densities (number per ha) were calculated from the following relationship: density =  $(10,000/S) (C/E)$ , where 10,000 is the number of m<sup>2</sup> in a ha,  $S$  = area sampled (m<sup>2</sup>) in a standard tow,  $C$  = mean number of juveniles captured per standard tow, and  $E$  = the trawl capture efficiency.

Multiple comparisons of mean catch per tow were made using the Kruskal-Wallis non-parametric test and significant differences were identified with Duncan's test. Paired comparisons were made with Mann-Whitney non-parametric test.

*Otolith Analyses.*—We estimated the timing of gag fertilization and settlement from daily increment analysis of otoliths, following the methods used by Brothers and McFarland (1981), Keener et al. (1988), and Strelcheck et al. (2003). We randomly selected either the right or the left lapillus from an individual and polished the otolith in the sagittal plane. Increment counts were made from each lapillus using a compound microscope (400× and 1000× magnification), with each increment equivalent to 1 d. The settlement marks on the otoliths (described in Keener et al., 1988) served as the endpoint for determining PLD. To determine fertilization date, we counted the number of increments between the otolith focus (center) and the settlement mark, and added 6 d to the total lapillus count to establish the presumed daily age based on the recommendations of Keener et al. (1988) for gag otoliths. Otoliths were read without information on the source of the otolith sample, thus eliminating counting bias with respect to temporal or geographic patterns. Only juvenile gag sampled through July of each year were aged (<200 increments) to minimize counting error, which increases with juvenile age (Ahrholz et al., 1995).

We tested for significant differences in fertilization dates, settlement dates, and PLD among years and regions using two-way analysis of variance. Significantly different means were identified with Tukey's test. We used a linear regression model to evaluate the relationship between PLD and fertilization date.

#### SPAWNING PATTERNS

To compare regional and temporal reproductive patterns in gag, we examined the reproductive status of adult gag from commercial hook-and-line and longline catches and from recreational charter boat hook-and-line catches from December 1997 through 1999. Fish caught north of 28° N (taken primarily by hook-and-line) were distinguished from fish caught south of 28° N (taken primarily by long-line gear). Fishermen provided information on the depth of capture and the location of capture to the nearest minute of latitude and longitude. Although they sometimes provided only approximate locations, the latitudinal distinction was always clear. To restrict the catch to only potentially spawning fish, we retained only females > 600 mm total length, TL, the approximate size-at-50% maturity (McGovern et al., 1998), and only those caught deeper than 50 m, the lower depth limit for spawning (Coleman et al., 1996).

All fish sampled were measured to the nearest mm TL. Gonads were removed, weighed, and examined both macroscopically and microscopically. All gonads were fixed in formalin, sectioned, and prepared for histological analysis following Collins et al. (1998). Gonads were staged histologically to determine reproductive states (Nikolsky, 1963; Hunter et al., 1992;

Garcia-Diaz et al., 1997). Active, but non-spawning females exhibited vitellogenic oocytes. Active spawning females had either hydrated oocytes or post-ovulatory follicles. Regressing females had notable atresia of vitellogenic oocytes. Fisher's exact test was used to compare the proportion of spawning to non-spawning females in each region for the initial months of the spawning season (December–February). We did not include fish that exhibited only primary growth oocytes because of our uncertainty about whether the fish were immature, developing, or inactive (i.e., mature but not spawning).

#### LARVAL TRANSPORT

The method of larval transport across the continental shelf from spawning sites to grassbeds is unknown. To evaluate the potential for near-surface horizontal transport of larvae, we used an empirical model of near-surface transport forced by daily winds (reanalysis winds, determined as the best fit of all available data, computed after the fact; from NOAA's National Center for Environmental Prediction <http://www.ncdc.noaa.gov>). To calibrate the model, we used observed surface currents, determined by ~600 satellite-tracked drifter buoys in the nearshore waters between the northwest Florida border and Cedar Key collected over an 13 mo period from 1996 to 1997 (Ohlmann et al., 2001; Sturges et al., 2001). The drifters extended from a few cm below the sea surface down to 1 m deep, and were tracked by the Service Argos satellite system (<http://noaasis.noaa.gov/ARGOS/>). They have a very small antenna to reduce windage effects.

Drifter motion was computed in longshore and cross-shelf components. We computed the longshore drifter motion parallel to the local bottom topography (the coefficients were determined on the basis of correlation with longshore winds). Because of the close proximity of the coast, we computed the cross-shelf (onshore) motion separately, using the wind component approximately 60° counterclockwise of the "onshore" direction. This wind angle had the highest observed correlation with onshore drifter motion at these depths. Combining these two components of drifter (or near-surface particle) motion provided the net motion. We found these correlations to be consistent for all frequencies in the so-called wind-driven band. On the west Florida shelf, periods of wind forcing range from a few days to approximately 3 wks. The coherence is high at all frequencies where the wind velocity is reliably above the noise level.

We used the computations of drifter motion as the basis for simulating trajectories of particle (larval) movement. We selected three starting positions for particles that represent likely spawning sites on the mid to outer shelf. These include two positions south of 28° N and one position north of 28° N. We computed drifter motions for four 2-mo overlapping periods. Using different start dates (in February 1, March 1, April 1, and May 1) and end dates (8 wks later) at each spawning site that approximate the period between spawning and settlement (although gag typically cease spawning by mid-April), we calculated likely trajectories of particles driven by surface currents. We generated progressive vector plots of simulated drifter motion beginning every 3 d and running for 2 mo for all years from 1989 through 1998, thus overlapping the available biological record of juvenile settlement time and abundance. The end-points of these trajectories (20 in all for each 2-mo interval for each group) define an area where wind could have transported surface-dwelling larvae during that 2-mo period. Because the winds are poorly correlated at times separated by > 3 d, each computed drifter track is therefore statistically independent of the previous one.

We also evaluated the likelihood that seasonal differences in oceanic transport explained the differential settlement patterns of juvenile gag along the Florida coast by calculating Ekman transport using hourly average wind speeds (Bakun, 1973; Schwing et al., 1996) from January through May of 1994 through 1998. These wind data originated from a single data buoy (NOAA National Data Center Buoy 42036), located about 100 nm offshore in the northern region at 28°30'22" N, 084° 30'37" W (<http://www.ndbc.noaa.gov>).

## SEAGRASS COVERAGE

Seagrass meadows provide important settlement habitat for juvenile gag (Koenig and Coleman, 1998). To evaluate the relationship between habitat availability and juvenile settlement patterns, we quantitatively assessed seagrass aboveground biomass bimonthly during the primary months of gag settlement from February through June each year in 1996 and 1997 at all sampling locations during collection of gag juveniles, and biweekly in 1999 at the northernmost and southernmost sampling locations (Fig. 1). At each location, seagrass was collected from five haphazardly placed quadrats (25 × 25 cm) at each of three replicate sites. Seagrass blades were cut just below sediment level and stored in plastic bags on ice (not frozen) until processed. In the laboratory, seagrass blades were washed in fresh water; dead blades, macroalgae, and belowground portions of blades were discarded. Samples were dried for 24 hrs at 60° C, rinsed in a 5% phosphoric acid solution to remove epiphytes, dried again for 24 hrs at 60° C, and then weighed to obtain the epiphyte-free above-ground dry biomass of seagrass blades m<sup>-2</sup> (g m<sup>-2</sup>). Bimonthly estimates of seagrass density during the primary months of gag settlement were pooled by month within each area for 1996 and 1997 to increase statistical power and precision. Samples from 1999, collected only from the latitudinal extremes of our sampling area, were analyzed separately. Data were not normal (Shapiro-Wilk Test) so the nonparametric Mann-Whitney Test was used to determine significance (P < 0.05).

## RESULTS

### FERTILIZATION AND SETTLEMENT

Fertilization and settlement dates among surviving juveniles on the west Florida shelf differed significantly among years and between regions (Tables 1,2; Fig. 2). Mean dates in the north were significantly later than dates in the south (Tables 1,2; Fig. 2) in all 4 yrs. Further, significant temporal differences in fertilization and settlement dates occurred between years (Tukey Test, P < 0.05) with earliest mean dates occurring in 1997 and latest dates in 1994 (Table 1). There was also a significant interaction between years and regions (Table 2) indicating that yearly means in fertilization and settlement times were not independent from the region effect.

North and south settlement differed by 13 d in 1994, 12 d in 1995, and 33 d in 1996 and 1997. The 1994–95 and 1996–97 settlement offsets were significantly different from each other as indicated by a significant interaction effect (Table 2). Although some fish began settling in March, settlement occurred primarily in April and May for both regions. Rarely did individuals settle before March (Fig. 2). There was some evidence of bimodality in fertilization and settlement dates for southern settlers in 1994 and in northern settlers in 1997 (Fig. 2). However, sample sizes were often too small (N < 30) to clearly discern modal patterns.

Table 1. Mean (standard error, SE) fertilization dates, settlement dates, and pelagic larval duration of gag (*Mycteroperca microlepis*) on the West Florida shelf. Dates are given as consecutive day, starting with January 1 = day 1. n = sample size.

Year	Region	n	Fertilization	Settlement	Pelagic duration
1994	North	7	91.4 (4.1)	128.3 (3.2)	36.9 (1.8)
1994	South	59	74.7 (2.2)	114.9 (2.0)	40.2 (0.5)
1995	North	46	77.8 (1.2)	121.2 (1.2)	43.4 (0.5)
1995	South	25	66.6 (2.9)	109.3 (2.0)	42.7 (1.2)
1996	North	14	90.8 (6.1)	131.6 (5.9)	40.7 (1.1)
1996	South	20	56.3 (5.1)	99.0 (5.1)	42.7 (0.8)
1997	North	45	73.5 (2.7)	115.6 (2.6)	42.1 (0.6)
1997	South	13	33.6 (8.9)	75.2 (8.9)	41.7 (0.9)



Table 2. Results of a two-way ANOVA comparing year (1994–1997) and region (north and south of 28°N latitude on the west Florida coast) for gag (*Mycteroperca microlepis*) fertilization date, settlement date, and pelagic duration.

Source	df	Fertilization date				Settlement date				Pelagic duration			
		SS	MS	F	P	SS	MS	F	P	SS	MS	F	P
Year	3	3,266.0	1,088.6	3.9	0.009	2,702.9	900.9	3.7	0.011	384.8	128.2	7.6	< 0.0001
Region	1	19,221.9	19,221.9	69.6	< 0.0001	18,260.9	18,260.9	76.7	< 0.0001	12.3	12.3	0.7	0.393
Interaction	3	4,378.2	1,459.4	5.2	0.002	4,149.4	1,383.1	5.8	0.001	98.4	32.8	1.9	0.123

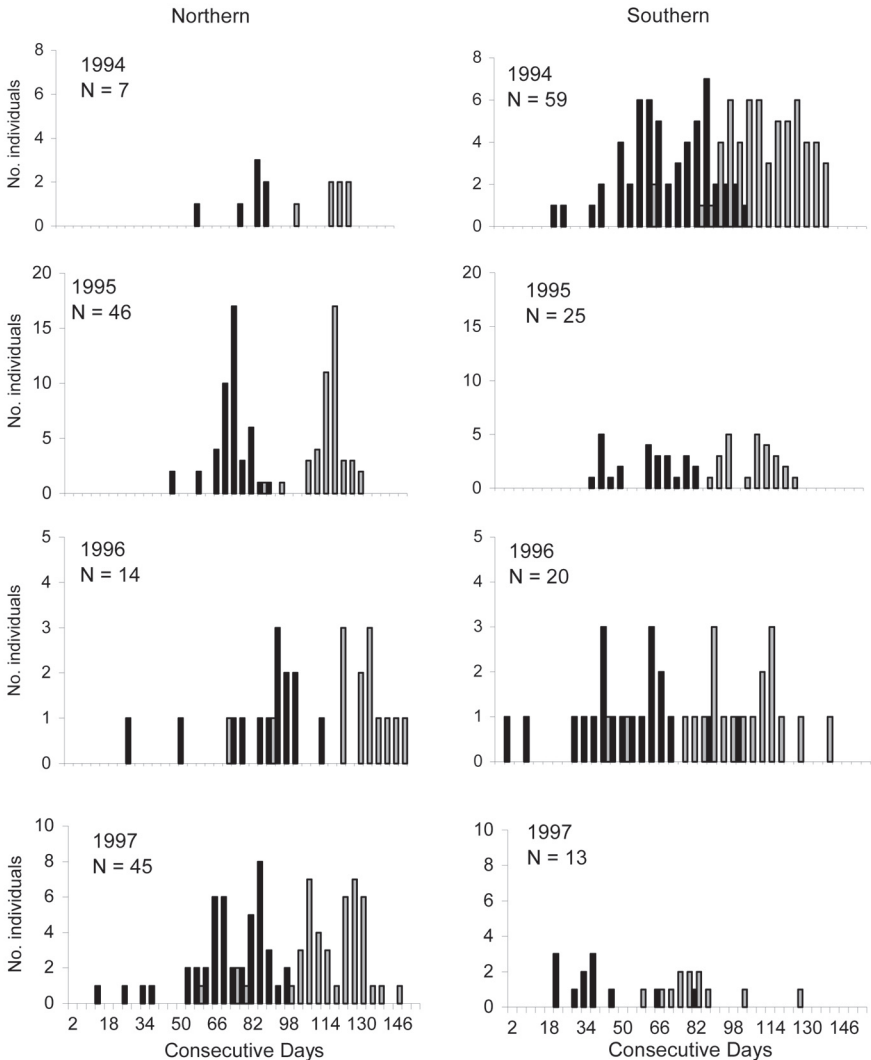


Figure 2. Fertilization (black bars) and settlement (grey bars) date distributions for juvenile gag *Mycteroperca microlepis* along two west Florida coastal regions, north of and including 28° N, and south of 28° N. 1994; 1995; 1996; 1997. Consecutive days cover the period from January 1 (1) through early June (154). One fish with a fertilization date in November and settlement date in mid December of 1996 (considered an early arrival in the cohort of the 1997 year class) was excluded from the graph.

Pelagic larval durations ranged from 29 to 52 d, and mean PLD for region and year ranged from 37 (North, 1994) to 43 d (North, 1995). No significant regional differences in PLD occurred within years and there was no significant interaction between regions and years (Table 2). There was a significant ( $P < 0.05$ ) negative relationship between PLD and fertilization date in 1994 and in 1995 (Fig. 3), but not in 1996 ( $y = 44.74 - 0.004x$ ,  $r^2 = 0.063$ ) or 1997 ( $y = 43.98 - 0.029x$ ,  $r^2 = 0.009$ ).



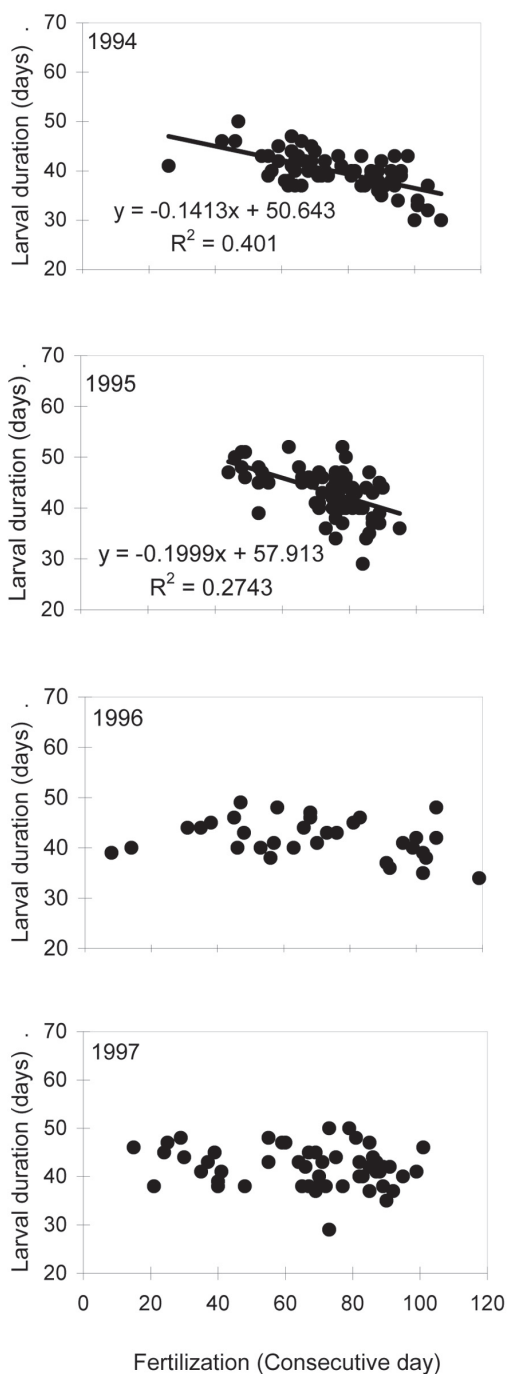


Figure 3. Regression of larval duration as a function of estimated date of fertilization determined from juvenile gag lapillar otoliths for years 1994–1997. Only in years 1994 and 1995 is the relationship significant at the  $P < 0.05$  level, with larval duration shorter in fish spawned later in the season.

Table 3. Abundance of juvenile gag sampled from seagrass beds along the west coast of Florida. The locations correspond to the black circles on Figure 1, respectively, from north to south. Fraction is the number of gag captured per number of standard tows (150 m at 1.0 kts); number in parentheses is the density in number per hectare. NS = no sample taken.

Sample Locations	1994	1995	1996	1997
St. Andrew Bay	NS	200/179 (93)	0/55 (0)	18/20 (75)
St. Joe Bay	NS	1/10 (8)	0/15 (0)	0/20 (0)
St. George Sound	9/73 (10)	19/31 (51)	7/66 (9)	8/20 (33)
Keaton Beach	0/4 (0)	0/10 (0)	14/45 (26)	0/20 (0)
Cedar Key	0/6 (0)	0/10 (0)	27/15 (150)	11/30 (31)
Anclote Key	11/6 (153)	4/22 (15)	9/25 (30)	9/35 (21)
Mean, North	20/89 (19)	224/262 (71)	57/221 (22)	46/145 (26)
Tampa-St. Pete Area	18/10 (150)	15/25 (50)	24/30 (67)	18/40 (38)
Sarasota Area	25/8 (260)	11/10 (92)	3/15 (17)	10/20 (42)
Pine Island Sound	46/19 (202)	68/40 (142)	52/84 (52)	55/100 (46)
Mean, South	89/37 (200)	94/75 (104)	79/130 (51)	82/160 (43)

JUVENILE DENSITY

Juvenile gag densities varied within and between regions among years (Table 3). Densities among southern locations were not significantly different within any year (Kruskall-Wallis,  $P < 0.05$ ), but were significantly different (Kruskall-Wallis,  $P < 0.05$ ) among years: densities in 1994 were significantly higher than in 1995 (Duncan's test,  $P < 0.05$ ) and densities in both years were higher than in 1996 and 1997 (which did not differ significantly from each other). Significant differences occurred within and among years at northern locations (Kruskal-Wallace,  $P < 0.05$ ), with densities significantly higher in 1995 (Duncan's test,  $P < 0.05$ ) than in the other 3 yrs. Mean juvenile densities were generally higher in the southern area than in the northern area during all 4 yrs (Mann-Whitney,  $P < 0.05$ ).

ADULT SPAWNING CHARACTERISTICS

Adult females sampled from offshore locations ( $> 50$  m depth) north ( $n = 32$ ) and south of  $28^{\circ}$  N latitude ( $n = 122$ ) generally showed similar patterns in gonad states across months (Fig. 4). The proportion of actively spawning to non-spawning females in the north versus the south were not significantly different in January, February, or March, but differed significantly in April (Fisher's exact test,  $P = 0.03$ ), the end of the spawning season. However, sampling times in April in the north were significantly earlier (Fisher Exact Test,  $P = 0.0004$ ) than in the south (89% were collected in early April in the north vs 42% in the south).

LARVAL TRANSPORT

The progressive vector plots indicate that almost all surface transport occurred to the north from all starting locations, regardless of month or year (shown here for only February–March 1996 for three different starting locations; Fig. 5B–D). This result is a function of the wind in the model computations and assumes that: (1) surface transport includes approximately the upper 1–2 m, (2) the velocity magnitude is relatively constant, and (3) the direction, top to bottom, may shift. A variety of previous studies (e.g., Price et al., 1987) has shown that the current direction varies from  $25^{\circ}$  to  $30^{\circ}$  clockwise of wind near the surface, to as much as  $60^{\circ}$  clockwise of wind

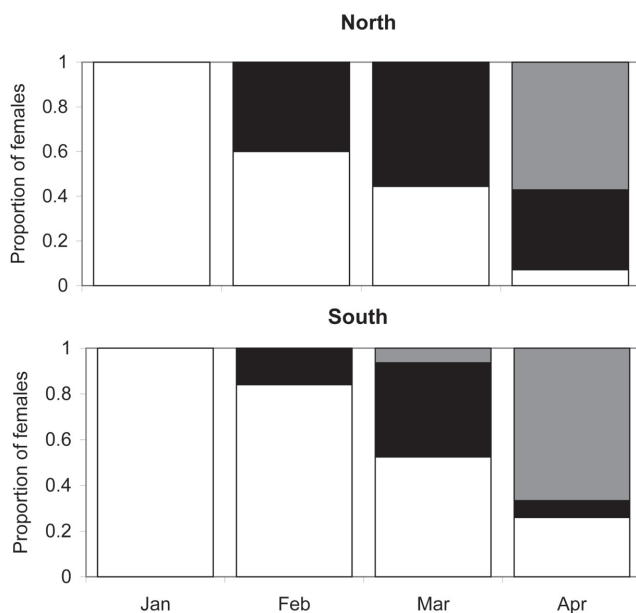


Figure 4. Gag (*Mycteroperca microlepis*) female reproductive state estimated by the percentage of actively spawning to non-spawning females in the north versus the south among collections from north and south of 28° N. Latitude on the West Florida Shelf in the northeastern Gulf of Mexico. White bars = active non-spawning. Black = active spawning. Grey = regressing (non-spawning inactive).

at depths of 10–15 m. Our calculations assumed very near surface motion, which is approximately 30° clockwise, but extending the results to slightly larger angles is straightforward. Based on these models, the greatest amount of northerly transport occurred in 1991 and the least in 1992.

A major result, based on these computations, is that no surface transport to the northern nursery grounds (> 28° N) could occur from spawning grounds located south of 28° N (i.e., starting locations 1 and 2). Even during 1991 when northerly transport was greatest, these calculations suggest that no particles from the south could reach near-shore waters in the north within the six weeks required for larval transport. Further, no particles could cross the shelf south of 28° N to reach southern nursery areas by relying on our computed wind-driven surface transport.

While variable, wind speeds were frequently stronger and winds were directed predominantly southward during January and February of 1994 through 1998, becoming somewhat lighter and more northward in March and April (Fig. 6A). Accordingly, Ekman surface transport was generally stronger during January and February than it was from March through May (Fig. 6B). Hence, the wind and Ekman transport vectors generally demonstrate a seasonal change from a predominant winter (January, February) to spring (March–May) pattern.

#### SEAGRASS COVERAGE

In 1996 and 1997, seagrass density north of 28° N was lowest in February and March, increasing thereafter to a maximum by June (Fig. 7A). Seagrass density south of 28° N was lowest in February, increasing thereafter to a maximum in May, then declining somewhat in June (Fig. 7A). While February seagrass densities were com-

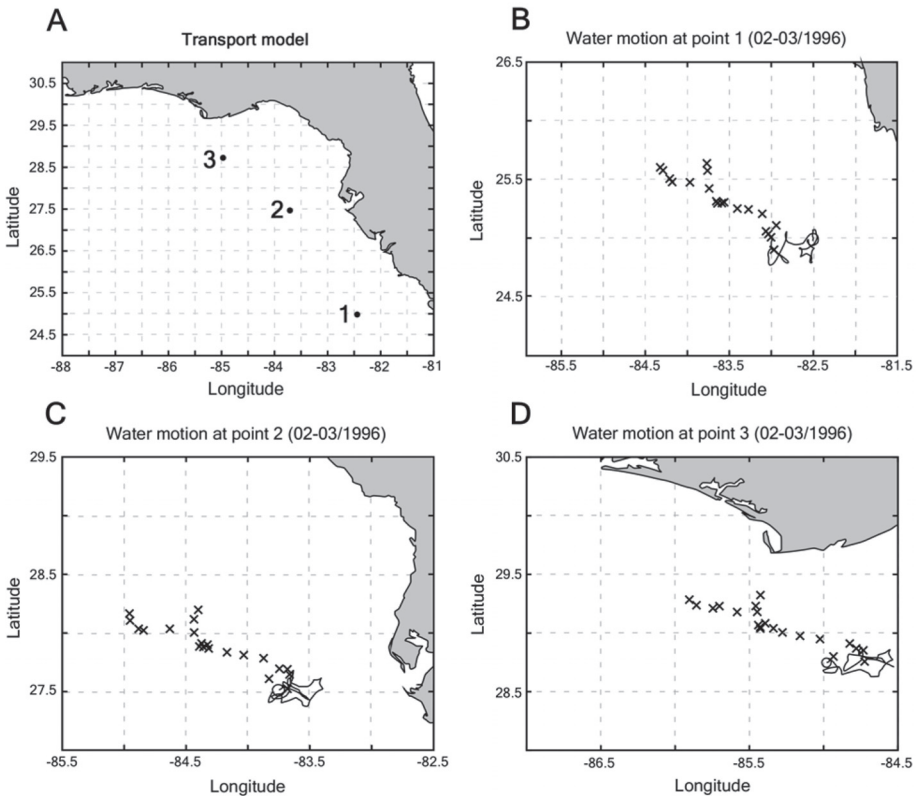


Figure 5. Near-surface wind driven transport of particles in the northeastern Gulf of Mexico for February through March 1996. A) starting locations for all simulations; B) simulations from starting location 1; C) simulations from starting location 2; D) simulations from starting location 3. Circle = starting location. The line traces the transport trajectory for a single simulation of particle motion calculated every 3 d over a 2-mo period. All other simulations in each frame are represented only by the endpoint (X).

parable between regions, seagrass recovery in the spring was faster in the south, and exceeded northern densities by April and May, the peak settlement period for gag.

The 1999 seagrass data indicated a similar pattern: comparable winter densities in both regions with more rapid growth and recovery early in the spring in the south. During peak settlement (April through May), however, regional differences in seagrass density had disappeared (Fig. 7b).

## DISCUSSION

Gag, like many tropical reef fishes (Cowen, 2002), exhibits relatively long PLDs (29–52 d) and transport distances (70–600 km) as a mandatory component of its life history in order to move from spawning habitat (shelf-edge reefs) to settlement sites (i.e., estuaries, specifically seagrass) (Coleman et al., 1996; Koenig et al., 1996; Koenig and Coleman, 1998). We found that gag exhibits consistent temporal (across years) and significant regional (north of 28° N versus south of 28° N) differences in mean fertilization and settlement dates. We also detected a trend, significant in some years (1994 and 1995), in which late-spawned gag larvae had shorter PLDs, although there was no regionally specific component to this.

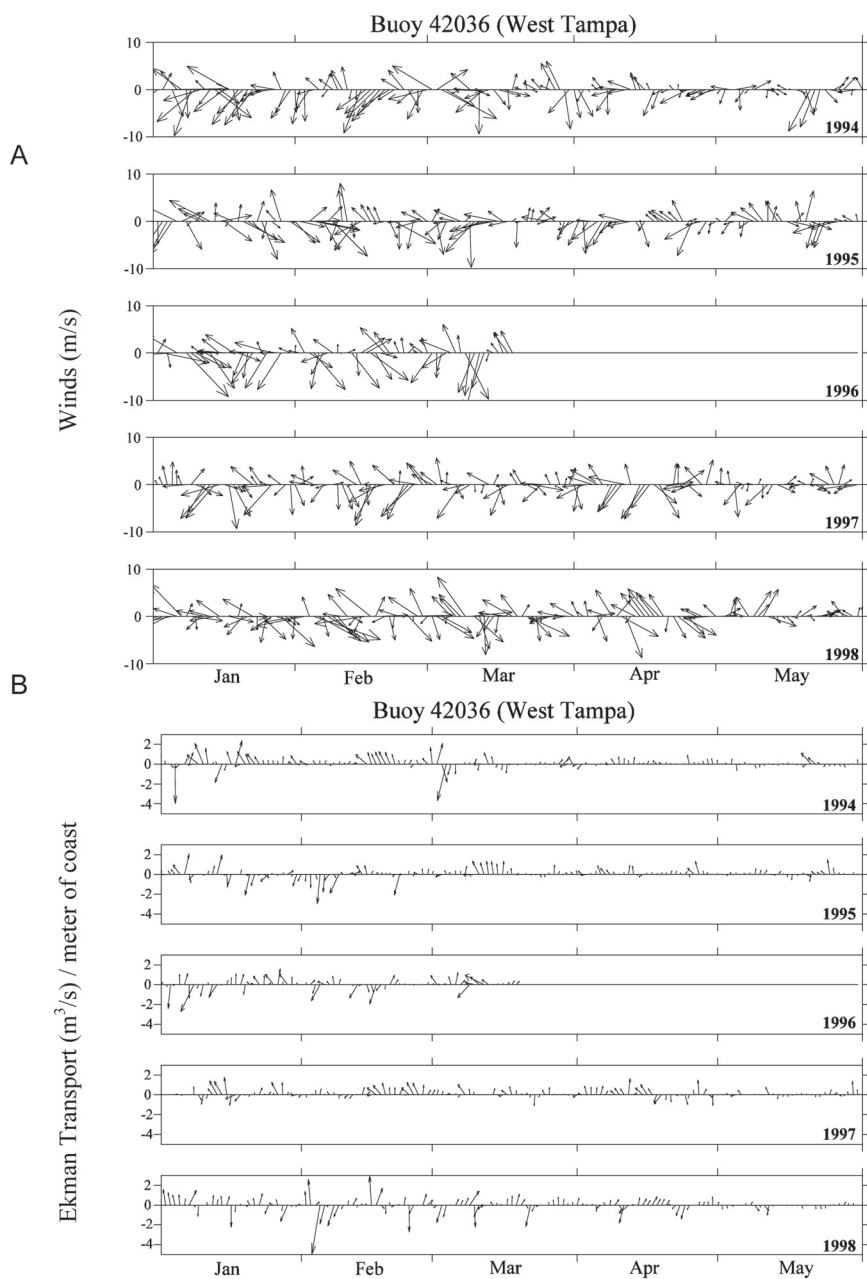


Figure 6. A) Observed wind and B) Ekman transport vectors for a location approximately 50 nmi south of Cape San Blas in the northeastern Gulf of Mexico (NDBC 32036). Vectors are “ocean convention,” i.e., direction blowing or transporting to. Data for days of the year 78–162 were not collected in 1996.

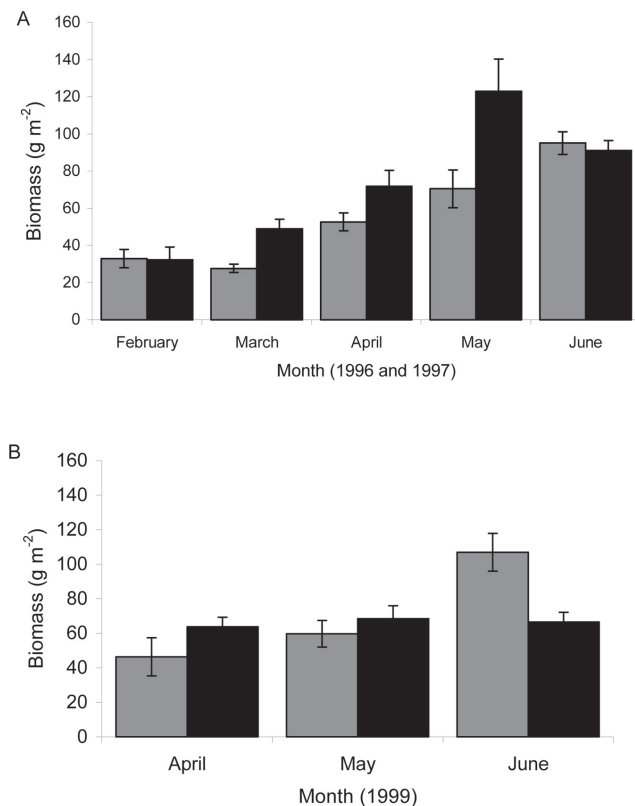


Figure 7. Monthly patterns of seagrass density determined: A) from nine sites sampled along the entire west coast of Florida from 1996 through 1997 separated into regions north (grey bars) and south (black bars) of 28° N; B) from the farthest north (St. Andrew Bay, 30° N, grey bars) and farthest south (Pine Island Sound, 26° N, black bars) sampled in 1999. Error bars indicate standard error of the mean. In panel A, means were significant for March and May and in panel B, means were significant for June.

Variable time to settlement (PLD) is common among reef fishes. Several families of reef fish have particularly variable PLDs [e.g., wrasses (Labridae), flatfish (Bothidae), and surgeonfish (Acanthuridae)], and some can extend their larval period to delay settlement and metamorphosis, thereby increasing their chances of surviving and finding suitable settlement habitat (Leis and McCormick, 2002). Length of larval life is closely coupled to larval growth. Searcy and Sponaugle (2000) found in the bluehead wrasse *Thalassoma bifasciatum* (Bloch, 1791), for instance, that PLDs were shorter in fast-growing spring-spawned than in slower growing fall-spawned fish. While the variability in gag PLD does not appear to contribute to the north–south settlement offset (no regional difference), it does suggest the possibility of a seasonally variable pelagic environment that either bestows faster growth on later-spawned fish or faster transport across the west Florida shelf.

Determining these and other key mechanisms affecting recruitment patterns of gag was beyond the scope of this study. However, we do investigate three possible mechanisms a posteriori in an attempt to explain the recruitment patterns we ob-

served: (1) regional differences in the timing of spawning, (2) regional differences in habitat availability, and (3) the potential for differential larval transport.

#### TIMING OF REGIONAL SPAWNING

The consistent offset in the timing of fertilization and settlement between northern and southern recruits to the west Florida coast suggests the possibility that spawning occurs earlier south of 28°N than it does north of 28°N. However, we found no corroboration between regional differences in fertilization dates and reproductive timing of adult gag collected off the West Florida Shelf. Rather, spawning increased in February, peaked in March, and declined in April, regardless of spawning location. This finding is consistent with previous studies conducted in the northeastern Gulf of Mexico (Hood and Schlieder, 1992; Coleman et al., 1996; Collins et al., 1998) and along the U.S. Atlantic coast (Collins et al., 1987; Keener et al., 1988; McGovern et al., 1998). The apparent regional difference we encountered in April is explained by differences in sampling time. That is, the north was sampled in early April, when spawning was tapering off, while the south was sampled later in the month, when spawning has largely ended (according to Coleman et al., 1996), thus giving the appearance of regional distinction.

#### HABITAT AVAILABILITY

An alternative mechanism to account for the apparent delayed settlement of juveniles in the north relative to the south relates to spatial and temporal differences in available habitat. If seagrass habitat in the north is more sparse in the winter and spring than that in the south, as suggested by Zieman and Zieman (1989), then it may prove unsuitable for early juvenile recruits, resulting in lower survival until late spring when seagrass regrowth occurs. Our seagrass density measurements indicated that seagrass densities were only slightly lower in the north relative to the south during settlement months (April through June). Whether this difference is sufficient to explain the observed differences in settlement is unclear. However, a more intensive examination of the early settling juveniles might provide clarification. For instance, if we could effectively capture pre-settlement juveniles and demonstrate that they arrive in the north as early as they arrive in the south (i.e., February) but do not successfully settle, that would indicate that conditions in the north are unfavorable to early settlement.

Regional patterns in seagrass coverage or other factors may contribute to the higher juvenile gag densities in the south relative to the north. It is possible that early settlers in the north experience higher mortality, and this reduces their overall abundance. Under this scenario, only later settlers would contribute to the observed densities. Because only the surviving settlers are sampled in our trawls, it would appear that settlement is later in the north. Factors other than seagrass density also may account for a possible limited survival of early settlers, including periodic low temperatures as weather fronts move through the area, and/or limited food resources in seagrass beds in the north relative to the south. To fully evaluate the possibility of differential settler mortality collections of juveniles must be made at or very near the time of settlement in both regions. This is very difficult in such large areas and our attempts at this failed.

Another possibility for higher juvenile densities in the south could be the limited spatial extent of seagrass habitats in the south relative to the north. In the north, the



Big Bend alone (3000 km<sup>2</sup>) accounts for more than all other west Florida seagrass habitat combined (excluding Florida Bay; Zieman and Zieman, 1989). A much larger cohort of settlers would be required in the northern seagrass beds to achieve the same densities as in the southern beds.

#### LARVAL TRANSPORT

Our numerical simulations using local wind forcing indicated relatively little cross-shelf transport either north or south of 28° N within the upper mixed layer and therefore the wind alone appears to be an unlikely mechanism for delivering larvae from spawning sites to the coast. We evaluated the consistency of this result by comparing it to our surface Ekman transport results (in the northern region only) and to the results from other studies describing current movement across the West Florida Shelf, including historical (1960s–1970s) drift bottle studies (Tolbert and Salsman, 1964; Williams et al., 1977), and recent (1996–1997) satellite-tracked drift bottle models (Yang et al., 1999).

Overall, our examination of current patterns revealed seasonal trends, but no annually consistent clear and abrupt change in patterns that would account for differential distribution of larvae and thus explain the differences in settlement time of juvenile gag. Ekman surface transport, though variable over the study, was relatively stronger early in the season (January–February) than later (March–May). Both historical (Tolbert and Salsman, 1964; Williams et al., 1977; Fig 10) and recent (Yang and Weisberg, 1999; Yang et al., 1999) studies show seasonal reversals in surface flow, with distinct winter (October–March) and summer (April–September) components (Yang and Weisberg, 1999; Yang et al., 1999). The winter pattern shows an anti-cyclonic gyre (the Big Bend Gyre) merging with northwestward flow from the south with offshore surface transport that could transport fish to the south, but not onto the shelf (similar to our numerical simulations), while the summer pattern features continuous northwest flow with surface transport onto the northwest Florida coast. Clearly, future investigations will require use of a three-dimensional model that evaluates water movements at various depths rather than just at the surface.

We infer from these calculations that advection in the offshore direction from the shelf *could* occur (see Yang et al., 1999), which would allow particle entrainment in the Loop Current, the Florida Current, and ultimately the Gulf Stream. In that way, eggs produced along the West Florida Shelf could provide recruits to the Florida Keys and Atlantic coast, as hypothesized by Powles (1977). Advection occurring early in the spawning season could explain why gag spawned in February typically do not appear north of 28° N.

We have assumed at this point that all juveniles settling along the west coast of Florida derive from a single source, spawning populations on the West Florida Shelf, and are therefore self-recruiting. However, a recent paper by Brule et al. (2003) describing gag spawning aggregations north of the Yucatán Peninsula suggests another possibility. Gag off the eastern portion of Campeche Banks (~21°–23° N) spawn roughly a month earlier than the gag on the West Florida Shelf. If the larvae resulting from these spawning events are transported from Campeche Banks to the southwest Florida coast, a distance of ~600 km, then these larvae could account for the earlier spawning and settlement dates seen in west Florida gag south of 28° N. Connectivity of Campeche Bank and South Florida oceanic regions by advective transport is clearly a possibility. Current intrusions onto the West Florida Shelf occur during the

spring–summer (Hetland et al., 1999; He and Weisberg, 2003), and particle movement studies conducted by Toner et al. (2003) suggest that intrusions are capable of transporting larvae from Campeche Bank to the west coast of Florida. It might be possible to investigate this mechanism using sea surface temperature (SST) records, although in many years the surface waters become so warm in the late spring and summer that SST is not a useful signal. We are currently studying this potential connectivity more closely by examining genetic relatedness of juvenile and adult fish from both oceanic regions.

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